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Nest-site selection by male Greater Rheas

Gustavo J. Fernández[1,3] and Juan C. Reboreda[2]

[1] *Instituto de Biología y Medicina Experimental-CONICET. Vuelta de Obligado 2490, 1428 Buenos Aires, Argentina and Laboratorio de Ecología, Programa de Ecología Matemática, Universidad Nacional de Luján, Rutas 5 y 7, 5700 Luján, Argentina*

[2] *Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EHA Buenos Aires, Argentina*

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ABSTRACT. Greater Rheas (*Rhea americana*) are ground-nesting birds that have high rates of nest desertion commonly associated with egg predation. We studied whether male Greater Rheas selected concealed sites to decrease detectability of their nests. We analyzed the spatial distribution of nests and compared the microhabitat characteristics of nest sites vs. sites selected at random, and sites of successful nests vs. sites of deserted nests. We also used experimental nests (nests without male attention) to assess whether egg losses were associated with the microhabitat characteristics of the nest site. The distribution of nest sites differed significantly from a random pattern, and nest sites had a higher percentage of shrub cover, a lower percentage of grass cover, and a higher concealment (low overall visibility) than sites selected at random. However, none of the microhabitat characteristics that we analyzed were associated with nest failure or the rate of egg loss. Experimental nests that were more visible tended to suffer higher and faster egg predation than less visible ones. Our results indicate that Greater Rheas selected concealed sites for nesting, but they did not get any apparent benefit for selecting these sites. We propose that habitat alteration and the type of predation that this species suffers at present may have reduced the benefits of selecting concealed sites for nesting.

SINOPSIS. **Selección de sitios de nidificación por machos de *Rhea americana***
El Ñandú Común (*Rhea americana*) es un ave que nidifica en el suelo y que tiene altas tasas de abandono de nidos, comúnmente asociadas con la predación de los huevos. Se estudió si los machos de Ñandú Común seleccionan sitios ocultos para reducir la detectabilidad de sus nidos. Se analizó la distribución espacial de nidos y se compararon las características de microhábitat de: 1) sitios de nidificación vs. sitios elegidos al azar y 2) sitios de nidos exitosos vs. sitios de nidos abandonados. También se usaron nidos experimentales (nidos sin la atención del macho) para evaluar si la pérdida de huevos estaba asociada con las características de microhábitat del sitio de nidificación. La distribución de nidos difirió significativamente de un patrón azaroso y fue consistente con un patrón uniforme. Los sitios de nidificación tuvieron un mayor porcentaje de cobertura de arbustos, un menor porcentaje de cobertura de pastos y un mayor grado de ocultamiento (baja visibilidad general) que los sitios elegidos al azar. Sin embargo, ninguna de las características de microhábitat analizadas estuvo asociada con el éxito de nidificación o con la tasa de perdida de huevos en los nidos. Los nidos experimentales más visibles tendieron a perder huevos a una tasa mayor que los menos visibles. Los resultados obtenidos indican que el Ñandú Común selecciona sitios ocultos para nidificar pero no obtiene beneficios aparentes por esta selección. Nosotros proponemos que la transformación del hábitat y el tipo de predadores que esta especie tiene en la actualidad pueden haber reducido los beneficios de seleccionar sitios de nidificación ocultos.

Key words: egg predation, nest concealment, nest distribution, nesting success, *Rhea americana*

For most bird species nest predation is the main cause of reproductive failure (Ricklefs 1969; Martin 1992, 1995). Because nest location can affect the risk of nest predation (Martin and Roper 1988; Kelly 1993; Stokes and Boersma 1998), selecting sites that reduce the chance of nest detection by predators would be an adaptive trait that must have evolved in many species of birds.

Nest sites are usually variable in their characteristics and, therefore, may differ in the probability of being detected by predators. After a review of 36 studies of breeding success in birds, Martin (1992) suggested that a major factor associated with nest fate is the degree of visibility. In the majority of ground-nesting birds, dense vegetation cover may provide nest protection from predators (Bowman and Harris 1980; Hudson 1982; Martin and Roper 1988; Martin 1993). Other nest characteristics that

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[3] Corresponding author. Current address: Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. Pabellón II Ciudad Universitaria, C1428EHA Buenos Aires, Argentina. Email: <gjf@bg.fcen.uba.ar>

influence breeding success are orientation (Austin 1976), height (Rendell and Robertson 1989; Wilson and Cooper 1998), and vegetation type and density (Selås 1996).

The pattern of spatial distribution of nests in precocial birds affects the risk of predation (Page et al. 1983; Picman 1988; Armstrong and Nol 1993). An aggregate pattern might reduce the risk of predation either by a dilution effect or by increasing the efficiency of nest defense (Andersson and Wiklund 1978; McLandress 1983). On the contrary, some experimental studies have found that high nest densities and a clumped distribution could increase the risk of predation, particularly in birds nesting in open habitats (Krebs 1971; Page et al. 1983; Martin 1988). Thus, individual birds may be selected to maximize the distance between their nests and those of neighbors, resulting in a sparse, dispersed nesting pattern.

Greater Rheas (*Rhea americana*) are large, flightless, ground-nesting birds, which inhabit grasslands, shrublands and open woodlands in South America. Their mating system combines harem polygyny and sequential polyandry (Brunning 1974). Adult males fight to monopolize a harem of females, with the dominant male excluding other males. The females lay between 20 and 30 eggs communally in a single nest. The male assumes the full incubation of the eggs for 36–45 d, and during this time he rarely abandons the nest for feeding (Fernández and Reboreda 1998). After laying eggs for one male, the females move on to lay eggs for another male (Bruning 1974). Once eggs hatch, males protect the chicks until they are 4–6 mo old (Bruning 1974; Fernández and Reboreda 1998).

In this species, approximately 65% of the nests are deserted (Fernández and Reboreda 1998), and nest desertion is associated with egg predation (Fernández and Reboreda 2000). The main egg predators are small and medium-sized mammals such as armadillos (*Chaetophractus villosus*), foxes (*Dusicyon gymnocercus*), and feral dogs (*Canis familiaris*), and raptors such as Crested Caracaras (*Polyborus plancus*) and Chimangos (*Milvago chimango*). Although small and medium-sized mammals hunt mostly by smell, they can also use visual cues to detect potential prey. In addition, until the end of the nineteenth century, adult rheas at the nest were preyed upon by visual predators such as cougars (*Felis concolor*) and jaguars (*Felis onca*) and also by Amerindians (Muñiz 1885). Therefore, we would expect that breeding rheas had been selected to prefer concealed nest sites to decrease detectability of their nests.

According to the "nest concealment hypothesis" (Filliater et al. 1994), we would expect a positive correlation between nest concealment and nest success (Clark and Shutler 1999). However, in disturbed areas, nest site selection could be constrained, and thus nest success could be affected by factors other than nest concealment such as rainfall or cattle disturbance (Fernández and Reboreda 1998, 2000).

We determined the spatial distribution of Greater Rhea nests and analyzed whether proximity to other nests was associated with nesting success. We also tested if Greater Rheas select for concealed sites for nesting by comparing the microhabitat characteristics of nest sites and randomly selected sites. In addition, we compared sites from successful and deserted nests and analyzed whether egg loss and nest desertion were inversely related to nest concealment. According to the "nest concealment hypothesis," we expect reduced concealment in deserted nests and a negative relationship between egg loss and nest concealment.

METHODS

Study area. The study was conducted in two contiguous cattle ranches of approximately 3500 and 800 ha (sites A and B, respectively) from September 1993 to January 1994. The number of rheas in sites A and B was approximately 250 and 150, respectively, with a sex ratio slightly biased towards males (55% males and 45% females). Less than 20% of the males attempted to reproduce during each breeding season, and only 5–6% of them were successful (Fernández and Reboreda 1998).

Our study area was situated near the town of General Lavalle in the province of Buenos Aires, Argentina (36°25′S, 56°56′W). The area is flat, low, and marshy, with little of the land rising more than 10 m above sea level. The study area corresponds to the southern temperate grasslands and is included in the so-called flooding pampas (Soriano 1991). The vegetation is composed of short grass species (*Bromus* sp., *Lolium* sp., *Paspallum* sp., *Cynodon* sp., *Sternotaphylum secundatum*), broad-leaved herbs

(*Atriplex* sp., *Dichondra* sp., *Oxalis* sp., *Plantago* sp., *Spergularia* sp., and *Trifolium* sp.), and scattered short bushes between 0.2–0.8 m high such as exotic thistles (*Cynara cardunculus*, *Carduus* spp.), cardas (*Eringium* sp.) and, less commonly, *Solanum glaucophyllum.* This region is used almost exclusively for cattle ranching.

Greater Rhea nests. Nests are built in open, higher grassland. The male selects a site and tramples down the vegetation within a circular area 1–1.6 m in diameter. Using alternate movements of the feet ("hollowing movements," following Bruning 1974) the male scrapes a depression edged with mounds of sticks, stems, and clumps of grass. During the egg laying and incubation periods, the male adds grass, feathers, dirt, and sticks to the border of the nest.

Nest spacing and nest characteristics. We conducted intensive nest searches throughout the breeding season (September to January). We found a total of 42 nests. We are confident that the number of nests we found was close to the actual number of nests in our study area (Fernández and Reboreda 1998). We mapped the nests on a 1:25,000 area map, and for each nest we calculated the distance to the nearest neighbor nest. We compared these distances with those distances between random sites ($N = 37$) and their nearest active nests. We determined the random sites by taking numbers from a random digits table and plotting the values in a X-Y coordinate system on a 1:25,000 area map. We discarded those sites that were in flooded areas, which were not suitable for nesting. The random sites were subsequently located in the field using cardinal compass points and physical references (distances from fences, crossing gates, windmills, artificial ponds, etc.).

For each nest and for 35 of the 37 random sites we measured the following microhabitat characteristics: 1) vegetation height, 2) distance to the nearest shrub, 3) percentage of grass, shrubs and herbs cover in a circle 4 m in diameter centered at the nest or random site, 4) depth at the center of the scrape (only for nests) and 5) nest concealment. Vegetation height was estimated as a weighed average of the height of grass, shrubs, and herbs (the height of each type of vegetation multiplied by its cover). Nest concealment was estimated by adding five Greater Rhea eggs at the center of the nest or random site and measuring the maximum distance at each of the four cardinal compass directions (N, S, W, E) at which the eggs were visible from an observer (GJF) at a height of 0.60 m (we considered this height as standard for measuring nest visibility). We estimated "overall visibility" and "visibility variation" of a nest or random site as the average and the standard deviation of the measurements respectively. For each nest and random site we also determined the minimum and maximum visibility as the least and most exposed view of the nest, respectively (Burhans and Thompson 1998).

To evaluate which variables were associated with the fate of the nest, we compared the microhabitat characteristics of nests that hatched chicks (successful) and nests that were deserted during incubation (deserted). For each nest we also measured the rate of egg losses during the incubation period (number of eggs lost per day) and analyzed the relationship between egg loss and nest-site characteristics.

We evaluated the risk of predation associated with nest concealment using nests without male attention (experimental nests). We placed between eight and 29 fresh Greater Rhea eggs in each of 12 nests that had been previously deserted by the male. For these experimental nests we used orphan eggs (see Navarro et al. 1998) and eggs from nests that were deserted during laying and early incubation. Eggs in these experimental nests were exposed to predators for 8–15 d. We measured the number of eggs lost per nest-day of exposure (number of days that the nest was under observation) and analyzed the association between the rate of egg loss and microhabitat characteristics. We also analyzed whether overall and minimum nest visibility influenced how long a nest remained without egg loss.

Statistical analysis. We determined the pattern of nest distribution using the Hopkins test (Krebs 1988). We used a discriminant function analysis (DFA) to evaluate whether any combination of microhabitat variables differentiated nest from random sites and successful from deserted nests. In order to select the variables for the multivariable analysis, we first performed univariate tests. For univariate statistical analysis we used nonparametric Mann-Whitney *U*-tests. In order to keep the statistical power >0.7, we set the level of significance at the $P = 0.05$ level for these analyses (Stevens

1996). We used similar univariate tests to select variables for the analysis of differences in microhabitat characteristics between sites with successful vs. deserted nests. Initial variables included in the DFA were: "grass cover," "shrub cover," "herb cover," "vegetation height," "overall visibility," and "visibility variation." Although we could not normalize the data, they were transformed to improve normality before performing the multivariate analysis. For all variables, Shapiro-Wilks *W* coefficients were significant, but most of them had values higher than 0.65 (except for shrub cover = 0.58 and herb cover = 0.33). Because a DFA typically is two-tailed, the smallest group had more than 20 cases, and we had few predictors, we assumed that the discriminant analysis was robust enough to failure from normality (Tabachnick and Fidell 1996). A similar multivariate analysis was performed to compare nest site characteristics of successful and deserted nests. For this analysis we added as predictors nest depth and distance to nearest shrub. The variables vegetation height and shrub cover were not included in the discriminant analysis of nest vs. random sites because they were correlated with overall visibility and grass cover, respectively ($r > 0.4$). Similarly, in the analysis of microhabitat characteristics of successful and deserted nests, distance to nearest shrub and grass cover were correlated with shrub cover, while vegetation height was correlated with overall visibility. Therefore vegetation height, distance to nearest shrub, and grass cover were not included in the analysis (Tabachnick and Fidell 1996). We used Spearman rank correlations to evaluate the relationship between egg loss and microhabitat variables in natural and experimental nests.

RESULTS

The average distance from a nest to its nearest neighbor was significantly larger than the average distance from a random site to the nearest nest (448.11 ± 58.01 m, $N = 33$ vs. 310.81 ± 36.84 m, $N = 37$; Mann-Whitney *U*-test, $Z = 2.31$, $P = 0.02$). In addition, the Hopkins index (estimated from a random sample of 20 nests and 20 random sites) differed significantly from a random pattern and indicated a tendency towards an uniform pattern (Hopkins index, $h = 0.528 < F_{40,40} = 0.532$, $P < 0.025$).

The fate of a nest was not associated with the fate of its nearest nest (Fisher's Exact test, $P > 0.99$). Proximity to a deserted nest did not affect nesting success. The distance between a successful nest and its nearest deserted nest was on average 456.25 ± 106.01 m ($N = 8$) while the distance between a deserted nest and its nearest deserted nest was 505.25 ± 72.09 m ($N = 30$, Mann-Whitney *U*-test, $Z = 0.16$, $P = 0.87$). In addition, proximity to a deserted nest was not associated with egg loss ($r_s = -0.24$, $Z = 1.1$, $P = 0.28$, $N = 21$).

Vegetation structure surrounding nests was significantly different from vegetation surrounding random sites. Nest sites had a higher percentage of shrub cover and a lower percentage of grass cover than random sites, but there was no difference in the percentage of herb cover (Table 1). Nest sites had higher concealment than random sites. Overall and minimum visibility were lower in nests than in random sites, while the visibility variation was significantly higher in nests than in random sites (Table 1). Site visibility was strongly associated with vegetation height ($r_s = -0.82$, $Z = 7.29$, $P < 0.001$, $N = 67$), but we did not find differences in vegetation height between nests and random sites (Table 1). One explanation for this result is that nest concealment is the result not only of the vegetation height but also of the depth of the scrape. The depth of the nest was negatively correlated with vegetation height ($r_s = -0.49$, $Z = 3.16$, $P = 0.002$, $N = 34$, Fig. 1). When we excluded nests that were more than 0.05 m deep from analysis, nest sites had a significantly higher vegetation height and visibility variation than random sites (Mann-Whitney *U*-test, $Z = 2.56$, $P = 0.01$; and $Z = 3.9$, $P < 0.001$, respectively; nest sites $N = 17$ and random sites $N = 31$ for both analysis). In this analysis overall visibility was marginally lower in nest than in random sites (Mann-Whitney *U*-test, $Z = 1.9$, $P = 0.06$, nest sites $N = 17$ and random sites $N = 31$).

In accordance with univariate tests, the discriminant function analysis indicated that overall visibility and visibility variation best differentiated nests from random sites (Table 2). Structure correlation between canonical variable scores and original variables characterized nest sites as having greater concealment ($r = -0.38$)

Table 1. Microhabitat characteristics (mean ± SE) of nest and random sites and successful and deserted nests. The number of nest and random sites were 42 and 35, respectively, while the number of successful and deserted nests were 8 and 29, respectively. Z values correspond to Mann-Whitney U-tests.

Microhabitat characteristics	Site			Fate		
	Nest (SE)	Random (SE)	Z (P)	Successful (SE)	Deserted (SE)	Z (P)
Grass cover (%)	84.8 (3.5)	96.3 (1.6)	2.34 ($P < 0.05$)	91.0 (4)	83.19 (4.19)	1.00 (NS)
Herb cover (%)	0.83 (0.55)	2.3 (1.45)	0.52 (NS)	0 (0)	1.05 (0.7)	1.07 (NS)
Shrub cover (%)	14.32 (3.46)	1.53 (0.7)	2.35 ($P < 0.05$)	9.0 (4.82)	15.76 (4.19)	0.76 (NS)
Overall visibility (m)	3.82 (0.28)	5.84 (0.65)	2.04 ($P < 0.05$)	3.7 (0.37)	3.85 (0.35)	0.69 (NS)
Maximum visibility (m)	4.63 (0.32)	5.9 (0.7)	0.17 (NS)	4.32 (0.45)	4.83 (0.41)	0.09 (NS)
Minimum visibility (m)	2.9 (0.22)	5.41 (0.74)	2.6 ($P = 0.01$)	3.11 (0.36)	2.82 (0.27)	1.21 (NS)
Visibility variation (m)	0.84 (0.08)	0.27 (0.08)	5.14 ($P < 0.01$)	1.24 (0.32)	2.02 (0.24)	1.4 (NS)
Nearest shrub (m)	11.43[1] (2.94)	15.53[1] (3.0)	2.05 ($P < 0.05$)	16.25[2] (6.25)	10.62[2] (3.28)	0.82 (NS)
Nest depth (m)	—	—	—	0.06[3] (0.02)	0.07[3] (0.01)	0.38 (NS)
Vegetation height (m)	0.15 (0.01)	0.13 (0.01)	1.39 (NS)	0.05 (0.01)	0.15 (0.01)	0.26 (NS)

[1] nest (N = 28), random sites (N = 15).
[2] successful (N = 4), deserted (N = 19).
[3] successful (N = 7), deserted (N = 27).

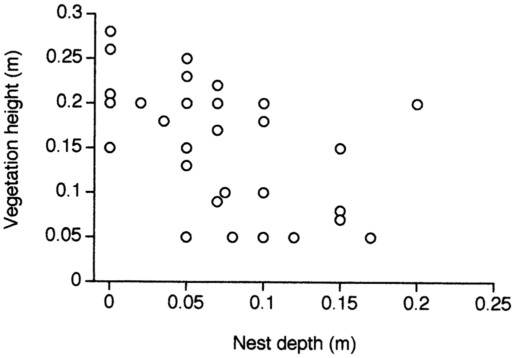

Fig. 1. Correlation between vegetation height and nest depth in Greater Rhea nests.

and higher visibility variation (r = 0.86) than random sites (Fig. 2a, Table 2).

We were unable to differentiate microhabitat characteristics between successful and deserted nests (Tables 1–2, Fig. 2b). Deserted nests suffered higher rates of egg loss than successful nests (0.043 ± 0.015 egg lost/nest-day, N = 10 and 0.006 ± 0.001 egg lost/nest-day, N = 8 respectively, Mann-Whitney U-test, Z = 2.5, P = 0.01), but the rate of egg loss was not associated with the microhabitat variables we analyzed (Table 3).

In the experimental nests without male attention, egg losses showed a tendency to increase with nest visibility (r_s = 0.52, Z = 1.7, P = 0.08, N = 12), and nests with higher visibility showed a tendency to suffer egg predation faster than nests with lower visibility (r_s = 0.55, Z = 1.7, P = 0.08, N = 12).

DISCUSSION

The distribution of nest sites differed significantly from a random pattern and was consistent with a uniform pattern. This type of distribution is also observed in a closely related species, the Ostrich, *Struthio camelus* (Bertram 1992), and it is common in territorial birds. However, unlike ostriches, which actively defend territories (Bertram 1992), Greater Rheas do not exhibit any territorial behavior that could explain the pattern of nest distribution. The only territorial behavior in this species is nest defense, but it is restricted to a few meters around the nest (Bruning 1974). Nest spacing does not appear to be related to nest success either, as proximity to the nearest deserted nest

Table 2. Structure correlations of the discriminant functions of nest site variables. The variables with significant contributions to the discriminant functions ($P < 0.05$) are underlined.

Microhabitat characteristic	Nest sites vs. random sites		Successful vs. deserted nests	
	r	*P*	*r*	*P*
Overall visibility		0.03	−0.0236	0.21
Visibility variation	−0.38	<0.0001	0.7903	0.04
Herb cover	0.86	0.16	—	—
Shrub cover	−0.25	0.27	0.3468	0.95
Nest depth	—	—	0.1375	0.61
Wilk's Lambda	0.59		0.63	
Approximate *F*-statistic	13.35		1.09	
P	<0.00001		0.42	

was not associated with nesting success. Armstrong and Nol (1993) suggested that a dispersed pattern would be an efficient anti-predator strategy to reduce nest detection. These results support the hypothesis that the fate of a nest was independent of the fate of its nearest neighbor.

Nest sites have a higher concealment than randomly selected sites. There is an association between nests and shrubs in spite of the fact that shrubs have low density and a highly scattered distribution. In addition, concealment is partially associated with type and height of vegetation. However, the negative correlation between vegetation height and nest depth would indicate that, in order to increase nest concealment, males must scrape deeper in sites with low vegetation height.

Other work that studied the breeding ecology of Greater Rheas mentioned nesting attempts in sites with high vegetation cover. Mercolli (1993) found that in the Chaco region most Greater Rhea nests were built in "Monte" clumps but not in the open areas that this species usually inhabits. Similarly, Coddenotti (1997) described nesting attempts in cultivated fields, which presumably have higher vegetation cover. Unlike these studies that were conducted in highly heterogeneous habitats, our study was conducted in a rather homogeneous habitat. However, our results also indicate that males select nest sites with higher concealment.

Although we found differences in microhabitat characteristics between nests and random sites, we did not find an association between nest concealment or other microhabitat characteristics and nesting success or egg loss in active nests. Thus, we were unable to identify predation risk as the selective force responsible for the development of the preference for concealed sites (Clark and Shutler 1999). However, there was a negative association between nest con-

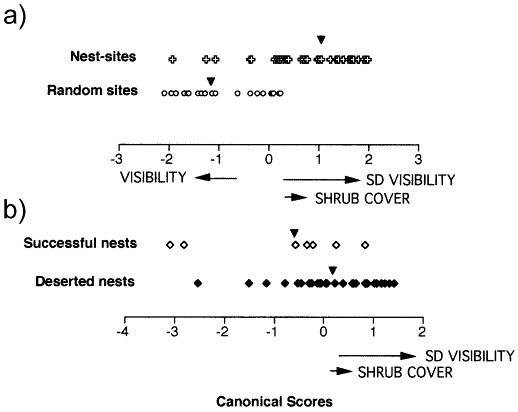

Fig. 2. Canonical scores and variable contribution of the discriminant analysis. a: nest vs. random sites, b: successful vs. deserted nests.

Table 3. Correlations between egg loss and nest microhabitat characteristics ($N = 21$ nests, except for nearest shrub where $N = 11$). For this analysis we did not use nests with herb cover.

Microhabitat characteristic	r_s	*P*
Grass cover	−0.13	0.17
Shrub cover	0.4	0.17
Overall visibility	−0.12	0.52
Visibility variation	0.29	0.19
Maximum visibility	−0.02	0.91
Minimum visibility	−0.25	0.21
Nearest shrub	0.13	0.72
Nest depth	−0.25	0.62
Vegetation height	−0.08	0.41

cealment and egg loss in the experimental nests without male attention. Although the results of predation experiments using artificial nests should not be overly generalized to infer predation rates at natural nests (Roper 1992), these results may be used to evaluate the effect of nest concealment on the probability of nest predation. In that sense, our study shows that experimental nests had a tendency to suffer higher and quicker egg predation. Because of our small sample size, the power of the statistical test of the effect of microhabitat characteristics on the egg loss of active nests was low. Therefore, we can not rule out that some relationship between microhabitat characteristics and egg loss could be significant with a larger number of nests.

Several hypotheses have been proposed to explain the lack of effect of nest-site characteristics on nesting success. Selection of nest sites could be influenced by preferences for abiotic factors that enhance incubation (e.g., soil texture and permeability or humidity, Halupka 1998; Clark and Shutler 1999). Alternatively, Vickery et al. (1992) suggested that the effect of nest concealment on predation might be related to the type of predation. Concealment could be important when predators are visually oriented (e.g., avian predators, Clark and Nudds 1991) but would be less effective when predators use olfactory and/or auditory cues (Vickery et al. 1992), when predation is incidental (Gottfried and Thompson 1978; Vickery et al. 1992; Wilson and Cooper 1998), or when there is a rich guild of predators (Filliater et al. 1994). In these cases, because of the diversity of predators, selection for any single habitat characteristic does not result in a reduction in the overall risk of nest predation (Filliater et al. 1994; Götmark et al. 1995; Wilson and Cooper 1998). However, this situation does not preclude that simple site selection rules could have evolved in response to a limited benefit in reducing the risk of nest predation (Filliater et al. 1994).

We propose that nest-site selection in Greater Rheas would be an adaptive trait for avoiding or reducing egg predation by small and medium-sized predators such as armadillos, foxes, and feral dogs. At present, these species are the main terrestrial predators of Greater Rhea nests in our study area. Nonetheless, the relationship between nest concealment and nest fate can be influenced by abiotic factors that affect nest desertion (e.g., there is a negative association between nesting success and rainfall, Fernández and Reboreda 1998). In addition, recent habitat alteration could have reduced the benefits derived from nest-site selection. In particular, because cattle grazing has affected vegetation cover used as concealment for nests, the effect of nest-site characteristics on nesting success could have been reduced.

Temple et al. (1999) showed that ground-nesting birds that nest in continuously grazed pastures have poor reproductive success because many nests are deserted or destroyed by livestock. In our study site, fields have low stock densities, and in most cases the ranchers do rotational grazing, which can reduce the impact of livestock on nesting birds (Rohrbaugh et al. 1999). Therefore, although cattle raising could be considered a factor affecting the fate of Greater Rhea nests, the extent to which this activity affects nest-site selection in this species remains unclear. Our data indicate that, despite recent habitat changes, Greater Rhea males still select for concealed nest sites.

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